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Scale-dependent habitat associations of a rapidly declining farmland predator, the Little Owl *Athene noctua*, in contrasting agricultural landscapes

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ABSTRACT

During the last half of century, agricultural intensification within European farmlands caused the deprivation of farmland biodiversity, including farmland birds. Since then different conservation measures have been introduced to reverse declining trends of these birds. Yet, variable success of these measures suggests that habitat management requires planning at appropriate spatial scales. In this study, we examine habitat associations of the Little Owl, a rapidly declining farmland bird, within the context of Central European farmland. We collected presence/absence data from three different countries (the Czech Republic, Slovakia and Hungary) and examined habitat associations within and between regions at three different spatial scales: nest site, home range and landscape. We show that certain habitat associations are shared across all study regions, namely those involving grasslands and farm buildings that are used for foraging and nesting, respectively. Inter-regional analysis reveals that grasslands, gardens/orchards and farm buildings are most important habitats at small spatial scales, whereas at large spatial scales, the owl is positively associated with open habitats in terms of arable fields. We suggest that conservation planning should take into account both regional and inter-regional aspects of a species' habitat associations to distinguish between common habitat requirements and local species-environment relationships.

1. Introduction

Radical and widespread changes in the structure of European farmland in the last 50 years have led to a rapid loss of farmland biodiversity (Donald et al., 2001; Benton et al., 2003), especially in the most intensively used agricultural regions (Tscharntke et al., 2005; Firebank et al., 2008; Tryjanowski et al., 2011; Sutcliffe et al., 2015). Farmland birds are important components for the functioning of agricultural ecosystems and serve as good surrogates for farmland biodiversity (Donald et al., 2001; Gregory et al., 2005) and high-nature value farmlands (Morelli et al., 2014). At the same time, farmland bird populations are heavily influenced by agricultural intensification, which has resulted in large-scale population declines and range contractions of several species across Western and Central European farmlands (Chamberlain et al., 2000; Donald et al., 2006). Special conservation concerns, species conservation action plans, and agri-environmental schemes have been designed to assist the recovery of farmland bird populations (Dicks et al., 2014). However, recent studies have revealed that the positive effects of the conservation measures are rather limited (Kleijn et al., 2001; Kleijn and Sutherland, 2003). It has been pointed out that management measures applied over national scales often are beneficial only locally due to distinct habitat associations exhibited by different populations of the same species (Whittingham et al., 2007). Thus, for conservation strategies to be effective, species-specific responses to environmental conditions should preferably be established at different

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spatial scales and involving ecologically contrasting regions (Whittingham et al., 2007; Sánchez et al., 2009; Koleček et al., 2015).

Habitat associations of species distributed over heterogeneous environments are a result of complex ecological processes operating at different spatial and temporal scales (Johnson, 1980; Wiens, 1989; Morris, 1992). In intensively used farmlands, with substantial loss and fragmentation of non-agricultural habitats and decreased landscape heterogeneity, the species are exposed to progressively larger proportions of unsuitable matrices. While the availability of suitable habitats serves as an important precursor of a species' distribution and population density, it is usually not clear what spatial scales to consider when assessing habitat suitability (Jeliazkov et al., 2016; Šálek et al., 2015a). Furthermore, for conservation purposes, it is essential to identify species-specific habitat association patterns of different populations, since local population processes may mask large-scale patterns of distribution and population density gradients. For example, local habitat associations could differ across regions due to local adaptations or variation in land use complexity.

The Little Owl (*Athene noctua*) is a sedentary nocturnal predator inhabiting variety of open and semi-open habitats, but in Western and Central Europe it is mainly associated with human-modified agricultural landscapes (Żmihorski et al., 2006; Šálek and Schröpfer, 2008; van Nieuwenhuyse et al., 2008). As many other farmland bird species, the Little Owl has suffered dramatic population declines across many European countries over the past 50 years (Cramp, 1985; van Nieuwenhuyse et al., 2008; Thorup et al., 2010). This negative trend is especially pronounced in Central Europe where a regional population decline of up to 79% has been recorded (Šťastný et al., 2006; Šálek and Schröpfer, 2008; van Nieuwenhuyse et al., 2008; Šálek, 2014) and the owl's distribution has become highly fragmented due to numerous local population extinctions (Żmihorski et al., 2006; Šálek and Schröpfer, 2008). The large-scale habitat loss and agricultural intensification of traditional farmland and pastoral habitats, which lead to food limitation, seem to be the key factor responsible for the marked species' decline in Central Europe (Génot and van Nieuwenhuyse, 2002; Šálek et al., 2010; Thorup et al., 2010). Thus, the Little Owl can be a suitable indicator of grassland habitats availability and agro-pastoral activities, which are known to be linked with farmland biodiversity.

The main objective of this study is to examine the habitat associations of the Little Owl in order to reveal the key habitat attributes at multiple spatial scales. Habitat associations of Little Owls have been usually studied at small geographical scales and/or with small sample sizes (e.g. Dalbeck et al., 1999; Kasprzykowski and Golawski, 2006; Żmihorski et al., 2012). Thus, it is still unclear if habitat selection processes in this species differ between spatial scales as well as between regions with contrasting environments and agricultural intensity. Here we investigate multi-scale habitat associations of Little Owls in three Central European countries, the Czech Republic, Slovakia and Hungary, which differ markedly in land-use composition as well as in the species' population densities. We hypothesise that the Little Owl habitat associations differ depending on i) the spatial scale and ii) the geographical region. At small spatial scales, habitat associations should reflect more flexible processes of nest-site selection (Chase, 2002). Consequently, Little Owls in the Czech Republic and Slovakia should be associated with similar habitats at the nest-site and/or home range scales due to high socio-ecological similarities between the two countries. In contrast, we predict that at large

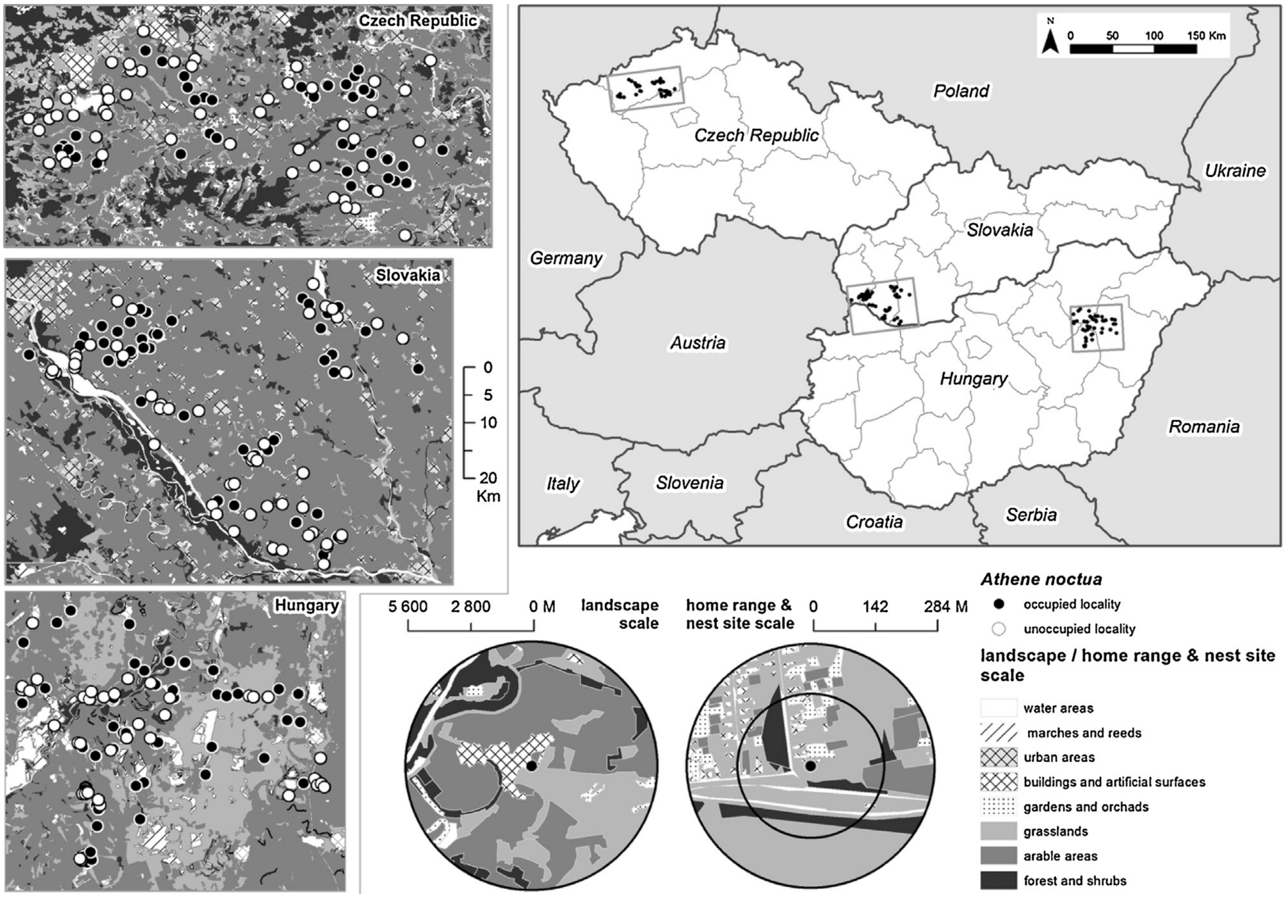

Fig. 1. Localization of the study regions in Central Europe and an example of habitat classification.

spatial scales owl populations in all regions should show similar habitat associations. This is because habitat associations at the large scales should reflect the processes of habitat selection, which are thought to be evolutionary more highly conserved. The results of this study may help to highlight the common conservation priorities of the rapidly declining Little Owl in Central Europe, but also identify important selection forces that the species faces at the regional level.

2. Methods

2.1. Study areas and species

To compare habitat selection of Little Owls in farmlands with different agricultural intensity, land-use composition and population density gradient, we selected three study regions located in lowland farmlands of Central Europe: 1) northern Bohemia, the Czech Republic (GPS: 50°23′N, 13°40′E), 2) south-western Slovakia, Slovakia (GPS: 48°2′N, 17°31′E) and 3) eastern Hungary, Hungary (GPS: 47°33′N, 20° 54′E) (see Fig. 1 and Table 1). The landscape structure and land-use composition of selected farmlands in the Czech Republic and Slovakia were highly modified by agricultural intensification especially during the last 60 years (e.g. Lipský, 2000). This resulted in large-scale reduction of natural and semi-natural non-cropped habitats, as well as an increase in soil fertilization and pesticides use, and the switch from spring to autumn sowing (Tryjanowski et al., 2011). In contrast, the study area in Hungary, which partially overlaps with the Hortobagy National Park, is characteristic by traditional agro-pastoral farming. This type of farming results in a high diversity of natural habitats, such as biodiversity-rich grasslands and extensively-used short-grass pastures. On the contrary, most of the agricultural areas of Central Europe, where intensification has taken place, had led to a decrease in the proportion of grassland habitats (see Table 1). Moreover, grasslands in the Czech Republic and Slovakia are mostly represented by intensively-used hayfields and small proportion of pastures. Most of hayfields have been drained and reseeded in the past and are currently managed by machine mowing twice a year. Crop fields in all study regions are predominantly used for intensive cultivation of cereals (especially winter cereals), oilseed rape, maize and legumes.

The Little Owl is a non-migratory and sedentary farmland predator with stable long-term territories of adults and low dispersal distances (<15 km) of offspring (Gassmann and Bäumer, 1993; van Nieuwenhuyse et al., 2008). It feeds on a high diversity of prey mainly represented by ground-dwelling animals (earthworms, large insect, small mammals), which are hunted from elevated hunting perches (Fajardo et al., 1998; Šálek et al., 2010; Romanowski et al., 2013). The population densities of the Little Owl in the study regions differ markedly (see also Table 1), with the lowest average population density recorded in the Czech Republic (0.29 calling males/10 km^2, Šálek, 2014) and Slovakia (0.92 calling males/10 km^2, Dobrý et al., 2012). In contrary, the average population density of the Little Owl recorded in the Hungary (5.01 calling males/10 km^2) indicates one of the highest population densities of this species from an agricultural landscape in Central Europe (van Nieuwenhuyse et al., 2008; Šálek et al., 2013). In the study regions, the species exclusively nests in human settlements, preferring human constructions, namely, farms and residential buildings (Dobrý et al., 2012; Šálek et al., 2013; Šálek, 2014).

2.2. Little Owl monitoring

Distribution and population density of the Little Owl was monitored during 2009–2014 using direct and indirect methods. During the spring period (March–April), the owls were monitored based on tape-recorded stimulation of the male territorial voice, which is the most widespread and efficient method used for the recognition of Little Owl's presence (van Nieuwenhuyse et al., 2008). The selected study period coincides with the peak of annual Little Owl's vocal activity (Exo, 1989). Playback monitoring was carried out just during favourable weather conditions (no heavy rain, strong wind or mist), from sunset until midnight, occasionally extending it into morning hours. In each location, the territorial voice of the Little Owl was broadcasted for two minutes and repeated three times, separated by a silent period of one minute between each repetition (Johnson et al., 2007). Most of the localities were visited repeatedly within one season. Since the species within studied regions is closely associated only with human settlements and has not been recorded in recent years (see above) in natural habitats within farmland landscape, we monitored its distribution only in human-dominated landscapes. This method was supplemented with acoustic monitoring using automatic digital recorders (Olympus DS-50, Olympus DM-650) and indirect methods such as searching for fresh food remains (pellets), moulted feathers and communication with local stakeholders.

2.3. Environmental analysis

The habitat selection of the Little Owls was studied using the comparison of occupied vs. unoccupied localities (presence-absence data), which is a standard methodological approach in habitat selection studies (Carroll et al., 1999; Whittingham et al., 2005) and was successfully used for analysis of habitat selection of Little Owls in other regions (Zabala et al., 2006; Šálek and Schröpfer, 2008). The centres of occupied localities were determined as places in Little Owl territories where a nest was found or where breeding behaviour was repeatedly recorded. The centre of unoccupied localities corresponds to a place, where territorial voice has been repeatedly broadcasted without a positive response (see also Šálek and Schröpfer, 2008). In total we used 50 occupied and 50 unoccupied localities for each region (n = 300) and the individual localities were randomly selected. To reveal scale-

Table 1
Land-use composition (%) and average population density (calling males/10 km^2) of the Little Owl in three study farmland regions in the Central Europe.

	Czech Republic	Slovakia	Hungary
Arable land (%)	78.7	82.4	36.0
Grasslands (%)	9.7	2.1	48.1
Woodland (%)	4.4	4.8	3.0
Water area (%)	0.2	3.0	4.5
Human settlements (%)	4.3	7.1	4.1
Gardens and orchards (%)	1.9	0.4	0.2
Artificial surfaces (%)	0.9	0.1	0.1
Marshes and reeds (%)	0.0	0.2	4.1
Study area (km^2)	1072.2	2091.6	611.3
Average population density (calling males/10 km^2)	0.29	0.92	5.01

dependent habitat selection of the Little Owls across the study areas, we used three spatial scales (see also Martínez and Zuberogoitia, 2004; van Nieuwenhuyse et al., 2008):

- Nest site scale (168 m radius, 8.9 ha) – represents a core area of Little Owl spatial and foraging activity (35% of the home range size, Exo, 1987; Finck, 1990; Génot and Wilhelm, 1993; Sunde et al., 2009), reflecting individual decisions on nest safety and the proximity to food resources.
- Home range scale (284 m radius, 25.3 ha) – the scale represents annual home range size of the Little Owl (Exo, 1987; Finck, 1990; Génot and Wilhelm, 1993; Sunde et al., 2009; Grzywaczewski, 2009).
- Landscape scale (5600 m radius, 100 km^2) – the scale represents broad landscape structure and composition around studied localities (Martínez et al., 2007).

Based on the literature search, we identified nine habitat variables that could be important predictors of Little Owl occurrence and population density at various spatial scales. In particular, we investigated proportion of grasslands, arable land, residential buildings, gardens and orchards, artificial structures, farm buildings, woodland, reeds and marshes, and water area (for detailed description and references see Table 2). The analysis of the proportion of individual habitat variables at nest and home range scales were performed by detailed digitalization of recent aerial ortho-photo maps (1:5000, GoogleMaps, 2013), using GIS (ESRI, 2014; QGIS, 2014). Habitat variables at the landscape scale were taken from 1:100,000 Corine Land Cover maps (Corine 2012).

2.4. Data analysis

PCA was used to examine the relationships between habitat attributes across all spatial scales within regions. The limit for the smallest eigenvalue was set to 1.5 for each analysis to reduce the number of principal components to the most important ones. PCA was calculated with Statistica (StatSoft, Tulsa, OK, USA). In order to reveal the importance of habitat attributes for Little Owl presence within and between three regions, we analysed the presence/absence data in four consecutive steps. First, we established the proportion of explained deviance for each habitat attribute and region (i.e. the Czech Republic, Slovakia, and Hungary). Hereby, each habitat attribute was examined simultaneously at all spatial scales (i.e. nest site, home range and landscape scales) and a smooth term of longitude and latitude was used as a covariate to control for spatial autocorrelation. Second, we sought the model best fitted to the data of Little Owl presence within regions. In order to address inter-correlations between predictors, we followed a forward-stepwise approach. Hereby, individual habitat attributes at all spatial scales were consecutively entered into the model in a descending order of their proportion of explained deviance. Third, the proportion of explained deviance for each habitat attribute was established at the level of all regions. Fourth, we sought the model best fitted to the data of Little Owl presence across all regions. Analogously as in the within-region analysis, individual habitat attributes at all spatial scales were consecutively entered into the model in a descending order of their proportion of explained deviance based on the results from the step three. Region identity was considered as a random factor to account for inter-regional variation in Little Owl presence.

Generalised additive models (GAM) with a binomial error distribution were used to address spatial autocorrelation in Little Owl distribution and potential non-linear relationships between Little Owl presence and ecological predictors (habitat attributes). The logic of GAM is similar to generalised linear models (GLM), with the main exception that the former is not limited to functions of parametric shape. GAM was used to model Little Owl presence as a smooth function of ecological predictors by employing penalized regression splines. GAM analyses were conducted with the mgcv package (Wood, 2011) in R (R Development Core Team, 2014). The mgcv package uses the gam function also for generalized additive mixed models (GAMM) with the possibility of inclusion of simple random effects by the re-smooth class (Wood, 2004). For the gam function, smoothness selection is obtained by a variety of estimation techniques, including maximum likelihood (ML) and restricted ML (REML). We tested the probability of Little Owl presence assuming a binomial distribution with the logit link and REML, which were used for the estimation of smoothing parameters. Forward stepwise selection was used to build optimal models and the "select" option, giving an extra penalty to each smooth term, was used as guidance for term exclusion during each step. The smooth interaction term of longitude and latitude was entered in the model during the first step because high degrees of freedom did not allow the term inclusion in later steps. This

Table 2
List of individual habitat attributes used as explanatory variables for analyses on the habitat associations of the Little Owl in three farmland regions in Central Europe.

Habitat variables	Description	Reason for inclusion (sources)
Grasslands	Proportion of different grassland habitats (e.g. meadows, pastures, lawns)	Various grassland types are the most important foraging habitat for Little Owls in Western and Central Europe (Dalbeck et al., 1999; Šálek and Lövy, 2012)
Gardens and orchards	Proportion of gardens and orchards with tree vegetation	Habitat selection for the orchards at local (Vossmeyer et al., 2006; Šálek and Lövy, 2012) and landscape spatial scale (Apolloni, 2013).
Arable land	Proportion of arable land	The arable habitats were most common habitat within the Little Owl territories (Grzywaczewski, 2009); however some crops are unsuitable foraging place during the breeding season (Finck, 1990). Increase of arable land has negative impact on Little Owl population density (Loske, 1986)
Woodland	Proportion of forest and shrub vegetation	Negative association with woodland vegetation at local and landscape scale (Zabala et al., 2006; Żmihorski et al., 2009; van Nieuwenhuyse et al., 2008; van Nieuwenhuyse and Bekaert, 2001; Żmihorski et al., 2012)
Residential buildings	Proportion of various residential objects (e.g. residential houses, multi-storey houses)	Higher proportion of buildings within the occupied territories (Źmihorovski et al., 2009; Šálek and Lövy, 2012)
Farm buildings	Proportion of various farm buildings (e.g. farms, cooperative farms, barns, hey sheds)	Important nesting places of the Little Owls in the Central Europe (Šálek and Schröpfer, 2008; Šálek et al., 2013; Šálek, 2014)
Artificial surfaces	Proportion of different artificial surfaces (roads, pavements, parking places)	Positive selection of artificial surfaces at home range and landscape scale (Šálek and Lövy, 2012), but Moreno-Mateos et al. (2011) found negative correlation of Little Owls with roads
Marches and reeds	Proportion of marches and reed vegetation	Strong negative selection for marshland (Fajardo et al., 1998)
Water area	Proportion of water area (e.g. artificial ponds, water reservoirs, rivers, streams, ditches)	Non-suitable habitat for Little Owl (Cramp, 1985)

Table 3
Principal component analysis (PCA) examining variation in the cover of habitat attributes within three study regions (Czech Republic, Hungary, Slovakia). Habitat attributes examined in PCA are described in detail in Table 2. Factor loadings > 0.70 are marked in bold letters.

a) Czech Republic

Factor Loadings (Varimax normalized), Extraction: Principal components

	Factor1	Factor2	Factor3	Factor4	Factor5	Factor6
Arable land 168m	−0.034071	**0.743610**	−0.338700	0.370835	0.260473	−0.144660
Residential buildings 168m	−0.305597	−0.392267	0.036100	−0.616157	0.104952	−0.129264
Farm buildings 168m	−0.132960	0.018815	−0.057627	0.079188	0.093124	**0.922701**
Woodland 168m	0.123650	0.054917	−0.078860	0.115492	**−0.900844**	−0.110844
Grasslands 168m	0.072517	**−0.864913**	−0.109862	0.159110	0.112143	0.170929
Gardens and orchards 168m	0.118786	−0.097839	**0.794991**	−0.145327	0.243890	−0.188627
Other 168m	0.013131	0.169100	0.012114	**−0.847617**	0.065015	0.168636
Marches and reeds 168m	0.236003	−0.254071	−0.061795	0.155506	0.025739	−0.031157
Water area 168m	−0.180238	−0.011464	0.511770	0.163943	−0.342842	−0.124015
Arable land 284m	−0.202303	0.667945	−0.410948	0.365564	0.318465	−0.183903
Residential buildings 284m	−0.374034	−0.414871	0.032398	**−0.700576**	0.126867	0.033698
Farm buildings 284m	−0.094637	−0.006789	−0.034569	0.021807	0.093922	**0.935928**
Woodland 284m	0.261406	0.026926	0.005748	0.077115	**−0.899744**	−0.054679
Grasslands 284m	0.217517	**−0.908713**	0.012406	0.036821	0.030733	0.087979
Gardens and orchards 284m	0.071143	0.011933	**0.825645**	−0.191872	0.260672	0.030469
Other 284m	−0.068151	0.031588	0.017460	**−0.841497**	0.041879	0.210179
Marches and reeds 284m	−0.057187	0.070715	0.004595	0.100826	0.015135	−0.215972
Water area 284m	0.024257	0.107217	**0.790367**	0.184450	−0.173461	0.074407
Arable land 5600m	**−0.958883**	0.110546	−0.022386	0.013922	0.133062	0.085811
Artificial surfaces 5600m	0.495621	−0.154674	0.105994	−0.136475	0.363805	−0.108255
Woodland 5600m	**0.700354**	−0.070453	−0.095109	−0.022962	−0.301936	0.021757
Grasslands 5600m	**0.825028**	−0.205331	−0.025424	0.163903	−0.251505	−0.120110
Gardens and orchards 5600m	−0.014036	0.327599	0.048688	0.012713	−0.057113	0.070740
Residential buildings 5600m	0.066037	0.059556	−0.042004	−0.570754	0.073456	−0.234239
Water area 5600m	0.588772	0.042625	0.254430	0.209684	0.111416	0.143609
Explained variance	3.241712	3.219515	2.603817	3.190168	2.455935	2.144293
Proportion of total	0.129668	0.128781	0.104153	0.127607	0.098237	0.085772

b) Hungary

Factor Loadings (Varimax normalized), Extraction: Principal components

	Factor1	Factor2	Factor3	Factor4	Factor5	Factor6
Arable land 168m	0.120601	**0.922767**	0.162203	−0.086445	0.036432	−0.041181
Residential buildings 168m	**−0.926502**	0.039167	0.076991	0.041286	0.031546	−0.103562
Farm buildings 168m	0.549923	−0.061433	0.057570	−0.074739	−0.606161	−0.109661
Woodland 168m	0.189037	−0.051336	0.001522	0.141291	−0.027953	**0.874581**
Grasslands 168m	0.418036	−0.631259	0.259535	−0.277192	0.047059	−0.443102
Gardens and orchards 168m	**−0.847315**	0.060829	0.070585	−0.073137	0.183038	−0.149646
Other 168m	−0.612858	0.040626	0.027427	0.036720	−0.525632	0.236313
Marches and reeds 168m	0.024280	0.021713	−0.028655	**0.900656**	0.049605	0.046797
Water area 168m	0.058999	0.013970	**−0.954965**	0.021042	0.075113	0.028839
Arable land 284m	0.235161	**0.918126**	0.196232	−0.109796	−0.040020	−0.052269
Residential buildings 284m	**−0.937708**	−0.040693	0.074780	0.070241	−0.002043	−0.159747
Farm buildings 284m	0.512188	−0.034691	0.069600	−0.010404	−0.691684	−0.168642
Woodland 284m	0.126462	−0.012997	−0.073251	0.128181	−0.112487	**0.922498**
Grasslands 284m	0.344620	**−0.739276**	0.241831	−0.278720	0.129358	−0.366315
Gardens and orchards 284m	**−0.858876**	0.010282	0.082147	−0.068896	0.105966	−0.192307
Other 284m	**−0.789905**	−0.085677	0.072956	0.092883	−0.420106	0.024815
Marches and reeds 284m	−0.014812	0.013257	−0.007832	**0.914975**	0.080063	0.092025
Water area 284m	0.057350	0.028683	**−0.943994**	0.034685	0.063072	0.019012
Arable land 5600m	−0.491395	0.535283	0.019053	0.285850	−0.374206	−0.260849
Artificial surfaces 5600m	−0.147896	−0.077811	0.043752	0.277701	−0.270711	−0.355773
Woodland 5600m	0.026939	0.058891	−0.138680	−0.245310	0.043976	0.348193
Grasslands 5600m	0.471654	−0.534083	0.187755	−0.128392	0.467747	0.137411
Marches and reeds 5600m	0.029138	−0.104870	−0.359982	−0.459042	0.138730	0.056288
Gardens and orchards 5600m	−0.056359	0.006063	0.085285	−0.066556	−0.370550	0.135971
Residential buildings 5600m	−0.026575	0.207722	−0.123373	0.082501	**−0.750944**	−0.043593
Water area 5600m	0.120449	−0.137207	−0.527566	−0.174180	−0.115389	0.167187
Explained variance	5.686044	3.319210	2.524643	2.380636	2.565991	2.541490
Proportion of total	0.218694	0.127662	0.097102	0.091563	0.098692	0.097750

c) Slovakia

Factor Loadings (Varimax normalized), Extraction: Principal components

	Factor1	Factor2	Factor3	Factor4	Factor5	Factor6
Arable land 168m	0.197059	**−0.710851**	0.285915	0.216252	−0.193247	0.371088
Residential buildings 168m	**−0.912795**	−0.074681	0.057760	0.008150	0.096698	0.048758
Farm buildings 168m	0.424154	**0.723078**	0.212502	0.105078	−0.052864	−0.064765
Woodland 168m	0.231477	−0.101361	**−0.794428**	0.101112	0.105475	0.275465
Grasslands 168m	0.332533	0.413388	0.047389	0.081683	0.077770	−0.679845
Gardens and orchards 168m	**−0.888572**	−0.157180	0.110833	−0.016280	0.112883	0.113100

Table 3 (*Continued*)

c) Slovakia

Factor Loadings (Varimax normalized), Extraction: Principal components

	Factor1	Factor2	Factor3	Factor4	Factor5	Factor6
Other 168m	0.070957	**0.810654**	0.117686	0.120423	0.007163	0.088830
Marches and reeds 168m	−0.007732	−0.117901	−0.058556	−**0.931796**	0.015209	0.048835
Water area 168m	−0.005389	−0.114189	−**0.700226**	−0.111270	−0.099359	−0.263910
Arable land 284m	0.422372	−0.584804	0.462976	0.149442	−0.291161	0.247173
Residential buildings 284m	−**0.930794**	0.030538	0.077580	0.016910	0.140314	0.012033
Farm buildings 284m	0.394455	**0.790661**	0.143897	0.073422	−0.073933	−0.059050
Woodland 284m	0.126803	−0.075905	−**0.781565**	0.097216	0.291730	0.217105
Grasslands 284m	0.177693	0.530953	−0.094676	0.068889	0.086615	−0.682724
Gardens and orchards 284m	−**0.883778**	−0.113564	0.106800	0.012394	0.141719	0.080351
Other 284m	−0.094052	**0.850671**	0.089754	0.119395	−0.000963	0.115311
Marches and reeds 284m	0.026065	−0.088948	−0.066885	−**0.947675**	0.041650	0.063456
Water area 284m	0.035040	−0.025281	−**0.764006**	−0.133086	−0.075496	−0.177211
Arable land 5600m	0.188340	0.041216	0.020174	0.462106	−**0.763453**	0.049541
Artificial surfaces 5600m	0.088662	0.124891	−0.271798	0.121690	0.593289	−0.158968
Woodland 5600m	−0.217101	−0.016476	0.019293	−0.080347	**0.877964**	−0.034180
Grasslands 5600m	−0.116330	0.021209	0.039511	−0.029671	**0.759276**	0.206789
Marches and reeds 5600m	0.002006	0.235234	0.015651	−0.056898	−0.031757	0.648638
Gardens and orchards 5600m	0.174569	−0.040164	0.140432	−0.005134	0.254749	−0.190250
Residential buildings 5600m	−0.077168	0.004198	−0.185371	0.394130	−0.364640	−0.377777
Water area 5600m	−0.302025	0.041283	−0.130242	0.073599	**0.794740**	−0.109188
Explained variance	4.282269	4.001221	2.899507	2.342281	3.432269	2.091438
Proportion of total	0.164703	0.153893	0.111520	0.090088	0.132010	0.080440

procedure was selected a priori also to control from the first step for the confounding effects of spatial distribution of Little Owls within regions. All analyses were performed on untransformed data so as to facilitate the interpretation of the results within and between regions (c.f. Zuur et al., 2009). Square-root transformation of the predictors would not qualitatively change our results, but the character of relationships would change in some cases. Specifically, some relationships would become non-linear after transformation. Since data transformation did not effectively fix the heterogeneity problem for our data, we performed our analyses on untransformed predictors. Finally, since GAM smooth terms are impossible to interpret without graphical presentation and most relationships appeared to have a linear trend, we also fitted our data with generalized linear models (GLM). This was done to address the robustness of GAM(M) results and provide parametric statistics for the optimal models selected by GAM(M). GLM(M) results were obtained for scaled and centred data with the stats (R Core Team, 2014) and the lme4 (Bates et al., 2014) packages in R.

3. Results

3.1. Regional and inter-regional variation in habitat attributes

The basic description of the three study regions in terms of 26 habitat attributes and the relationships between them are reported in Table 1 and 3. The PCA results revealed that within regions the cover for the same habitat attributes correlate positively between the nest site and home range scales, but not between the smaller scales and the landscape scale (Table 3). We also identified several influential correlations between different habitat attributes within regions. First, the cover of arable land at the nest site scale correlates negatively with (a) the cover of grasslands at the nest site and home range scales for the Czech Republic and Hungary and (b) the cover of farm buildings at the nest site and home range scales for Slovakia (Table 3). Second, for the Czech Republic, the cover of water area correlates positively with the cover of gardens and orchards at the nest site and home range scales (Table 3). Third, the cover of arable land correlates negatively with the cover of grasslands at the landscape scale, though this applies mainly to the Czech Republic and Slovakia (Table 3).

3.2. Importance of habitat attributes within regions

Despite inter-regional variation in their extent, the cover of grasslands, arable land and human constructions (farm buildings, residential buildings and artificial surfaces) consistently explained most of deviance in the presence of Little Owls in all regions (Appendix A). The cover of gardens and orchards also were major explanatory variables, but notably so only for Hungary and Slovakia. In turn, the cover of woodland (shrubs and trees) efficiently explained Little Owl presence only in Hungary and the Czech Republic. Finally, geographic location played a significant role in explaining variance in Little Owl presence in all countries, particularly in the Czech Republic where the Little Owl population is distinctly fragmented (Appendix A).

In order to see the relative importance of individual habitat attributes within regions, different habitat attributes were examined jointly (see Table 4). The probability of Little Owl presence in each region increased with the cover of grasslands at the scale of home range. The probability of the owl presence increased also with the cover of farm buildings, but this relationship occurred within regions at different scales – at the home range scale in Hungary and Slovakia, and at the nest site scale in the Czech Republic. The cover of gardens and orchards positively predicted the presence of Little Owls within regions, but again at different scales – at the nest site scale in the Czech Republic, at the home range scale in Hungary and at the landscape scale in Slovakia. In the Czech Republic and Hungary, the probability of Little Owl presence decreased with the increasing cover of woodland at the home range scale. In turn, the probability of Little Owl presence varied with the cover of arable land, but only in the Czech Republic and Slovakia. Specifically, the probability of the owl presence increased with the cover of arable land at the home range and the landscape scale. In addition, in Slovakia only, the probability of Little Owl decreased with the increasing cover of arable land at the nest site scale. The effect of water area played a significant role only for the Czech Republic with the probability of Little Owl presence increasing with water cover at the nest site scale. Finally, the cover of artificial surfaces played a significant negative role at the

Table 4
Generalised additive (GAM) and generalised linear (GLM) models on the probability of Little Owl presence within three farmland regions of Central Europe (Czech Republic, Hungary, Slovakia). GAM models are optimal models obtained by forward-stepwise selection. GLMM models are shown to allow comparison of GAM models with their parametric counterparts.

Parameters of GAMs					Parameters of GLMs				
(a) Little Owl in the Czech Republic (N = 100)									
	Estimate	SE	z	P		Estimate	SE	z	P
Intercept	−0.89	0.84	−1.06	0.29	Intercept	−0.65	0.52	−1.26	0.206
	edf		Chi square	P					
s(Farm buildings 168m)	1.63		6.34	0.012	Farm buildings 168 m	2.20	0.78	2.80	<0.010
s(Woodland 284m)	1.67		6.45	0.012	Woodland 284 m	−2.47	0.90	−2.74	<0.010
s(Arable land 284m)	0.93		9.38	<0.001	Arable land 284 m	6.13	2.23	2.74	<0.010
s(Arable land 5600m)	0.94		9.79	<0.001	Arable land 5600 m	4.80	1.55	3.09	<0.010
s(Grasslands 284m)	2.24		10.94	<0.001	Grasslands 284 m	6.21	2.22	2.79	<0.010
s(Water area 168m)	1.16		5.13	0.016	Water area 168 m	3.13	1.34	2.34	0.019
s(Gardens and orchards 168m)	0.83		3.76	0.023	Gardens and orchards 168 m	2.04	0.96	2.13	0.033
Model accuracy = 96%, AIC = 48.24					Model accuracy = 92%, AIC = 47.72				
(b) Little Owl in Hungary (N = 91)									
	Estimate	SE	z	P					
Intercept	1.32	1.11	1.19	0.236	Intercept	1.54	0.77	2	0.045
	edf		Chi square	P					
s(Grasslands 284m)	0.94		9.44	<0.001	Grasslands 284 m	6.47	2.04	3.17	<0.010
s(Woodland 284m)	0.90		5.03	0.012	Woodland 284 m	−1.90	0.91	−2.09	0.036
s(Farm buildings 284m)	2.02		8.79	<0.010	Farm buildings 284 m	1.30	0.51	2.53	0.011
s(Gardens and orchards 284m)	0.90		5.77	<0.010	Gardens and orchards 284 m	1.15	0.66	1.75	0.081
Model accuracy = 95.6%, AIC = 28.48					Model accuracy = 91.2%, AIC = 39.79				
(c) Little Owl in Slovakia (N = 100)									
	Estimate	SE	z	P					
Intercept	−0.90	0.60	−1.49	0.135	Intercept	−0.08	0.36	−0.22	0.824
	edf		Chi square	P					
s(Farm buildings 284m)	1.55		4.60	0.038	Farm buildings 284 m	0.56	0.38	1.46	0.143
s(Artificial surfaces 5600m)	0.87		5.21	0.011	Artificial surfaces 5600 m	−0.66	0.43	−1.51	0.132
s(Arable land 168m)	1.01		7.74	<0.010	Arable land 168 m	−2.46	0.81	−3.03	<0.010
s(Arable land 284m)	0.94		11.51	<0.001	Arable land 284 m	2.72	0.74	3.67	<0.001
s(Arable land 5600m)	2.72		11.19	<0.010	Arable land 5600 m	1.13	0.50	2.25	0.025
s(Grasslands 284m)	0.92		8.02	<0.010	Grasslands 284 m	1.21	0.45	2.68	<0.010
s(Gardens and orchards 5600m)	0.92		8.54	<0.010	Gardens and orchards 5600 m	1.03	0.46	2.24	0.025
Model accuracy = 91%, AIC = 67.57					Model accuracy = 87%, AIC = 79.92				

edf = estimated degrees of freedom; s(. . .) = smooth terms of predictors; AIC = Akaike information criterion; Model accuracy refers to the proportion of correctly classified presence and absence cases.

landscape scale, but only in Slovakia. Spatial correlation did not contribute significantly to explaining Little Owl presence within regions when multiple habitat attributes were considered jointly.

3.3. Inter-regional importance of habitat attributes

Similarly as for within-region analyses, the cover of grasslands, arable land and farm buildings explained most of deviance in the presence of Little Owls in inter-region analyses (Appendix A). The cover of woodland was another habitat attribute, which alone explained a considerable proportion of deviance between regions (Appendix A). The model best fitted to the data of Little Owl presence in the three regions revealed the significant importance of three habitat attributes at the scale of home range, two habitat attributes at the scale of nest site and one habitat attribute at the landscape scale (see Table 5). Specifically, the probability of Little Owl presence at the home range scale increased with the cover of grasslands, gardens and orchards (Fig. 2) and arable land and at the home range and landscape scale it increased with the cover of arable land. At the nest site scale, the cover of farm buildings

Table 5
Generalised additive mixed (GAMM) and generalised linear mixed (GLMM) models on the probability of Little Owl presence in three farmland regions of Central Europe (Czech Republic, Hungary, Slovakia). GAMM model is the optimal model obtained by forward-stepwise selection. GLMM model is shown to allow comparison of GAMM model with its parametric counterpart.

Parameters of GAMM					Parameters of GLMM				
	Estimate	SE	z	P		Estimate	SE	z	P
Intercept	−20.05	2.87	−7.14	<0.001	Intercept	−0.10	0.69	−0.15	0.880
Grasslands 284m	1.01E-004	1.28E-005	7.87	<0.001	Grasslands 284 m	4.78	0.62	7.70	<0.001
Arable land 168m	−9.16E-005	2.71E-005	−3.38	<0.001	Arable land 168 m	−1.46	0.43	−3.37	<0.001
Arable land 284m	7.77E-005	1.24E-005	6.26	<0.001	Arable land 284 m	4.21	0.68	6.21	<0.001
Arable land 5600m	1.10E-007	1.99E-008	5.50	<0.001	Arable land 5600 m	2.10	0.40	5.23	<0.001
	edf		Chi square	P	Farm buildings 168 m	1.18	0.29	4.03	<0.001
s(Farm buildings 168m)	1.30		36.24	<0.001	Gardens and orchards 284 m	1.75	0.32	5.46	<0.001
s(Gardens and orchards 284m)	2.70		41.22	<0.001				z	P
s(Country) – random intercept	1.84		18.40	<0.001	Country – random intercept			1.23	0.219
Model accuracy = 86.6%, AIC = 201.2, N = 291					Model accuracy = 85.2%, AIC = 210.2, N = 291				

edf = estimated degrees of freedom; s(. . .) = smooth terms of predictors; AIC = Akaike information criterion; Model accuracy refers to the proportion of correctly classified presence and absence cases.

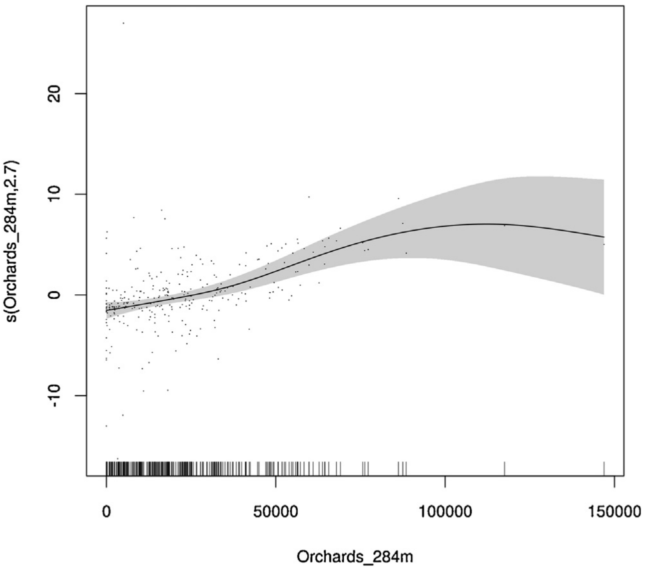

Fig. 2. Relationship between the cover of gardens and orchards at the home range scale and Little Owl presence at the inter-regional level. The plot illustrates how the probability of Little Owl presence changes relative to its mean with changes in the cover of gardens and orchards. The value of 0 on the Y axis represents mean probability of Little Owl presence; the Y axis is on the logit scale. The line shows REML estimates, and grey shaded area depicts 95% confidence intervals.

positively predicted Little Owl presence. In contrast, at the same scale, the probability of Little Owl presence decreased with the increasing cover of arable land. Finally, the probability of Little Owl presence varied significantly between regions and region identity was therefore included as a random effect in the optimal model.

4. Discussion

Spatially comprehensive analysis of species habitat-association patterns serves the conservation community to understand species-specific habitat requirements and provides key information for effective species conservation. Our inter-regional study of a rapidly declining Little Owl reveals that the species' associations with several key habitat attributes differ depending on the spatial scale and region. The percent cover of grasslands, arable land, gardens and orchards and farm buildings are generally most important habitat attributes at smaller spatial scales. At large spatial scales, the owl is positively associated with open habitats in terms of arable fields.

The grassland habitats have been known to be primary foraging habitats for Little Owls in Western and Central Europe, as revealed by radio-telemetry (Génot and Wilhelm, 1993; Šálek et al., 2010; Šálek and Lövy, 2012) and local habitat-selection studies (Exo, 1983; Dalbeck et al., 1999; Ille, 1996; Šálek and Berec, 2001). Our study corroborates these findings at the home range scale for both the regional and inter-regional data. Several studies have documented that the abundance of earthworms, insect and rodent species is higher in grasslands than in other habitats, such as arable fields (Russell, 1973; Exo, 1992; Ille and Grinschgl, 2001; Apolloni, 2013). Indeed, our analyses show that the relationships between the cover of grasslands and arable land are negative at small spatial scales. This indicates that the positive association with grasslands can be due to the owl preference at the nest-site scale for grasslands over arable fields. Previous studies found that the proportion of suitable grassland habitats may be a direct surrogate of the large-scale population density of Little Owls in agricultural landscape (Exo, 1983; Dalbeck et al., 1999; Vossmeyer et al., 2006). This work implies that the Little Owl density index can be assessed more accurately if the proportion of grassland habitats is assessed at the home range scale of the owl. That is, finer-scale spatial analysis may be needed for establishing more reliable density indices for this owl species.

After controlling for regional effects, the percent cover of gardens and orchards at the home range scale has been shown as another generally important habitat attribute for Little Owls (see also Šálek and Lövy, 2012; Apolloni, 2013; Habel et al., 2015). Yet, the association of the Little Owl with gardens and orchards varied inter-regionally with respect to the spatial scale. Moreover, while the cover of gardens and orchards correlates positively at the nest-site and home range scales, the cover of this habitat attribute at the landscape scale does not correlate with other habitat attributes and appears to reflect a unique landscape feature. Consequently, the positive association of Little Owls with the cover of gardens and orchards at the landscape scale in Slovakia can be attributed to the association of the species with rural areas rather than with the habitats with a specific cover of woody vegetation. High-stem gardens and orchards with a high proportion of old fruit trees and a high availability of natural hollows were described as an important nesting habitat for Little Owls. However, in the recent decades, this pattern seems to hold true only for the owl populations in Western Europe (Vossmeyer et al., 2006; van Nieuwenhuyse et al., 2008; Habel et al., 2015). In contrast, the Little Owl in Central and Eastern Europe dominantly nest in artificial constructions, such as farm buildings (see below). In Central Europe, the positive association of the species with gardens and orchards, as revealed in this study, may rather reflect the preference for high-quality foraging habitats composed of the mosaic of trees and short vegetation (Šálek and Lövy 2012; Apolloni 2013) and/or the avoidance of urbanised landscapes (see below).

The increasing cover of woody habitats at the home range scale decreased the probability of the Little Owl presence, but only in the Czech Republic and Hungary. Similar results for the Little Owl were reported also in local habitat-selection studies from Poland (Żmihorski et al., 2009; Żmihorski et al., 2012), Spain (Zabala et al., 2006), and Belgium (van Nieuwenhuyse and Bekaert, 2001). Woodlands seem to be inappropriate foraging grounds for Little Owls (Żmihorski et al., 2009), but they can also be avoided due to a higher predation pressure and antagonistic interspecific interactions, e.g. with the Tawny Owl *Strix aluco* (Mikkola, 1976; van Nieuwenhuyse et al., 2008; Zabala et al., 2006). Importantly, in addition to the results of inter-regional analysis, the negative association with woodland habitats was not revealed for Slovakia, which is similarly as the Czech Republic, more forested than the study area in Hungary. Therefore, the probability of Little Owl presence may not be a simple function of woodland cover. Nevertheless, the Little Owl habitat in neither study region comprises extensive proportions of forests, so the avoidance of woodland habitats can be statistically less likely to be detected.

The avoidance of closed woody habitats is indirectly suggested by the positive association of the Little Owl with arable habitats at large spatial scales. This result is in line with the assumed evolution of Little Owls in open and semi-open areas including arid lands, steppes and stony deserts (Schönn et al., 1991) and in the deforested and agricultural areas of Central Europe following the hypothesised postglacial colonization of Central Europe by humans (Pellegrino et al., 2014, 2015). As expected, our results revealed a stronger association of Little Owls with arable land in the Czech Republic and Slovakia than in Hungary, indicating a lower availability of suitable open habitats in the former two regions. Yet, at the smallest spatial scale, the habitat association with arable land showed the opposite trend in both the regional and inter-regional analyses. Namely, the probability of Little Owl occurrence was negatively associated with the percent cover of arable land at the nest-site scale. This result can reflect the negative relationship between the cover of arable fields and human settlements, the latter habitat representing the dominant nesting habitat in Central Europe (Šálek and Schröpfer, 2008; van Nieuwenhuyse et al., 2008). Indeed, PCA for Slovakia revealed strong negative relationships between the cover of arable land at the nest site scale and the cover of farm buildings at the nest site and home range scales. Consequently, this study indicates that the Little Owl in all the three Central European regions, but particularly in Slovakia, can be nest-site limited. We propose that conservation efforts in Central Europe should consider increasing nest-site availability particularly in the landscapes showing sufficient habitat openness.

The cover of farm buildings has been revealed as an important habitat attribute at the smaller spatial scales across all study regions, even though some of the relationships between the Little Owl occurrence and the cover of farm buildings were non-linear. Farm buildings are known to be the main nesting objects for the Little Owl in Central Europe (van Nieuwenhuyse et al., 2008). This pattern has also been confirmed by nation-wide monitoring in the Czech Republic and Slovakia. Specifically, 72% and 51% of the nesting sites of the Little Owl in the Czech Republic and Slovakia, respectively, were detected within farm buildings (Šálek and Schröpfer, 2008; Chrenková in litt.). Similarly, for the Hungarian study area, 40% of the presumed nesting sites were recorded in farm buildings, and 83% of the farms visited were occupied by Little Owls (Šálek et al., 2013). Farm buildings offer a high diversity of nesting sites (barns, storages for hay and grains, animal sheds) not only for Little Owls, but also for other farmland nocturnal predators with conservation concern, such as the Barn Owl *Tyto alba* (Poprach, 2008). Importantly, local farming management may also contribute to the Little Owls' positive association with farm buildings. Previous studies have documented that Little Owls prefer farms with active management, namely, agricultural objects with animal husbandry (Šálek et al., 2013; Šálek, 2014). Such farms are associated with grain spillage, silage holes, grain storehouses, manure heaps, or a variety of short-sward pastures and hayfields, which provide a high diversity of food resources for farmland birds during the whole year (Hole et al., 2002; Hiron et al., 2013; Šálek et al., 2015b).

5. Management and conservation implications

Our results suggested large habitat plasticity of the species within studied regions in Central Europe that is further confirmed by various radio-tracking studies (see Finck, 1990; Génot and Wilhelm, 1993; Grzywaczewski, 2009; Šálek and Lövy, 2012), which followed fine scale habitat selection of Little Owls. Thus, conservation activities should be focused on increasing the habitat heterogeneity in order to ensure enough foraging opportunities and resources during the whole year. However, this study also highlights the crucial importance of grassland habitats, including the mosaics of gardens and orchards with herb understory, and the habitat comprising farmland constructions. The mosaic of these habitats appears to provide crucial foraging and nesting opportunities for Little Owls at the home range scale. Moreover, conservation measures should be conducted mainly in farmland areas showing an extensive cover of open habitats, with arable fields representing these habitats in Central Europe.

Our regional analyses imply that grasslands are especially important in intensively used farmland regions of the Czech Republic and Slovakia. Surprisingly, the importance of grassland habitats at the home range scale has been revealed also for the Hungarian study area, which is characterised by an extensive cover of traditionally used steppe-like grassland habitats. Therefore, in order to support the declining Little Owl populations, it is crucial to halt any further loss and degradation of various grassland habitats even in regions showing large proportions of grassland habitats. We propose that the special conservation interest should be focused on the management and the restoration of pastures and hayfields that have been substantially degraded by eutrophication and reseeded with nitrogen mixtures. Management activities mimicking historical small-scale farming methods (e.g. strip-mowing or spatio-temporal diversification of mowing), should be used to enhance the biodiversity of grasslands and orchards (Čížek et al., 2012). Population collapse of Little Owls in Central European farmland has been attributed to the large-scale disappearance of traditional pastoral management of grassland habitats (van Nieuwenhuyse et al., 2008; Thorup et al., 2010; Šálek and Lövy, 2012). In fact, the high population density of Little Owls in the Hungarian study area can also be due to the prevailing commonness of traditional pastoral management of grassland habitats (see also Šálek et al., 2013).

The regional analyses indicate some distinct habitat associations with woodland, urban and water habitats. First, the owl in the Czech Republic and Hungary, but not in Slovakia, shows a negative association with woodland habitats. These results point to potentially important antagonistic interspecific interactions with woodland animal species and/or the co-variation of the woodland cover with the cover of other habitat attributes, e.g. the cover of human settlements. Second, the Little Owl was negatively associated with the cover of artificial surfaces at the landscape scale, but only in Slovakia. This result is important because it implies that increase in artificial surfaces of the countryside can be one of the factors contributing to the population decline of the Little Owl in Slovakia and other European countries. Finally, the Little Owl in the Czech Republic appears to associate with areas comprising of more extensive cover of water at the nest site scale. This is an unexpected result because the Little Owl is known to avoid wetland areas. In fact, the results of inter-regional and PCA analyses suggest that a larger cover of gardens and orchards can be the cause behind the positive association, because the cover of water and gardens and orchards correlate positively at the nest site and home range scales in the Czech Republic. Thus, researchers and conservation professionals should exercise a great caution when their inference is solely based on regional analyses.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agee.2016.03.031.

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